

STUDIES IN THE NOMENCLATURE AND CLASSIFICATION OF THE BACTERIA

II. THE PRIMARY SUBDIVISIONS OF THE SCHIZOMYCETES

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Since the definite recognition of the fact that bacteria, for the most part at least, are to be classed with plants rather than with animals, several names have been proposed to designate the entire group. The following may be noted:

Schizomycetes Naegeli 1857, p. 760.

Bacteriaceae Cohn 1872 a, p. 237.

Bacteria Cohn 1872b, p. 136.

Schizomycetaceae DeToni and Trevisan 1889, p. 923.

The bacteria as a group have received different ranking from various workers. Their exact position in the botanical scheme has also received different interpretations. Some authors have regarded the bacteria as constituting a family, others have called the group an order, still others a class. The most commonly accepted ranking at the present seems to be to place the *Schizophyceae* (blue green algae) and the *Schizomycetes* as coördinate classes of the phylum *Schizophyta*. The name *Schizomycetes* apparently has priority as a class name, and is entirely suitable and valid. It may be characterized as follows:

Schizomycetes Naegeli (1857, p. 760) char. emend. Migula (1894, p. 235)

Typically unicellular plants, cells usually small and relatively primitive in organization. The cells are of many shapes, spherical, cylindrical, spiral or filamentous; cells often united into groups, families or filaments; occasionally in the latter showing some dif-

ferentiation among the cells, simulating the organization seen in some of the blue-green, filamentous algae. No sexual reproduction known. Multiplication typically by cell fission. Endospores are formed by some species of the *Eubacteriales* (see below), gonidia (conidia, arthrospores) by some of the filamentous forms. Chlorophyll is produced by none of the bacteria (with the possible exception of a single genus). Many forms produce pigments of other types. The cells may be motile by means of flagella; some of the forms intergrading with the protozoa are flexuous, a few filamentous forms (as *Beggiatoa*) show an oscillating movement similar to that of certain of the blue green algae (as *Oscillatoria*).

The bacteria have been subdivided in many different ways. Cohn (1872) recognized four main divisions, or families, as he termed them; *Spherobacteria* for the cocci, *Microbacteria* for the short, non-filamentous rods, *Desmobacteria* for the longer, filamentous rods and *Spirobacteria* for the spiral forms. Later, in his classification of 1875, the bacterial genera were distributed under the two tribes into which he divided the *Schizophyta* (comprising both the blue green algae and the bacteria). The tribe *Gloeogenae* included those forms in which the cells are not united into filaments and the tribe *Nematogenae* those in which the cells occur in filaments.

Winter (1879) did not recognize groups among the bacteria higher than the genus, except that he placed the genera *Sphaerotilus* and *Crenothrix* in an "Anhang" to the bacteria.

Zopf (1883) subdivided the bacteria into four families, *Coccaceen*, *Bacteriaceen*, *Leptothricheen*, and *Cladothricheen*. The first family included only *Leuconostoc*, a spherical organism occurring in chains, the remaining families all included cocci, short rods, long rods and filaments and, in the last family named, spirals, as stages in the growth of the organism. The second showed no differentiation of base and apex of filament, the third showed a contrast between base and tip and the fourth showed pseudobranching.

De Bary (1884) used as a primary division the ability of the organisms of one group to develop endospores and of the other to produce arthrospores.

Zopf (1885) expanded his classification of bacteria, but used the same four main divisions as in his earlier discussion (1883).

Hueppe (1886) followed De Bary in dividing the bacteria into two groups, those forming endospores and those with arthrospores. The family *Leptotricheen* is given as an Anhang. Later (1891) he abandoned the scheme here outlined as a primary grouping.

Flügge (1886) divided bacteria into those which are spherical, rod shaped, spiral and those with variable growth forms.

The work of Winogradsky (1888) on the sulphur bacteria emphasized their importance as a group perhaps coördinate with the true bacteria.

Schroeter (1886) divided the class *Schizomycetes* into three orders: *Cocobacteria* for the spherical forms, *Eubacteria* for the rod forms, and *Desmobacteria* for the larger filaments, usually possessing a definite sheath.

De Toni and Trevisan (1889) divided the family *Schizomycetaceae* into three subfamilies (equivalent to the orders of Schroeter). These are: *Trichogenae*, the filamentous, frequently sheathed bacteria; *Baculogenae* with isolated rod shaped cells or with cells in chains (not filaments); and *Coccogenae* with spherical cells.

Ludwig (1892) recognized as the primary divisions cocci, rods and filaments (usually sheathed).

Thaxter (1892) called attention to the existence of a very distinct group of bacteria which he included in his family, *Myxobacteriaceae*. These organisms are characterized by the development of a pseudoplasmodial motile stage and a fruiting stage in which complex fruiting structures resembling those of the slime molds are formed.

Hueppe (1895) used five coördinate divisions (families) *Coccaceae*, *Bacteriaceae*, *Spirobacteriaceae*, *Leptothricheae* and *Cladotrichaeae*.

Migula (1894, 1895, 1897) also recognized five families of bacteria, *Coccaceae*, *Bacteriaceae*, *Spirillaceae*, *Chlamydobacteriaceae* and *Beggiatoaceae*.

Fischer (1895) divided the bacteria into the two subclasses

Haplobacteriacei and *Trichobacteriacei*. The latter included those types whose vegetative phase consists of unbranched or branched filaments or chains of cells, the individual members of which break off as swarm spores or gonidia, the former those whose cells are not typically filamentous.

Lehmann and Neumann (1896) divided the microorganisms included by most authors among the bacteria into three coordinate groups, *Schizomycetes* or fission fungi (true bacteria), *Hyphomycetes* (later *Actinomycetes*) or thread organisms showing true branching and the *fission algae* including other filamentous forms evidently closely related to the algae.

Chester (1897) recognized six orders (families) of bacteria, *Coccaceae*, *Bacteriaceae*, *Spirillaceae*, *Mycobacteriaceae*, *Chlamydo-bacteriaceae*, and *Beggiatoaceae*.

Jennings (1899) proposed that the two principal groups of the bacteria should be *Paraschizae* and *Diaschizae*, to include organisms which multiply by longitudinal and by transverse division respectively.

Migula (1900) divided the class *Schizomycetes* into two orders, the *Eubacteria* or true bacteria and the *Thiobacteria* or sulphur bacteria.

Kendall (1902) used in the main the classification proposed by Chester, but merged the family *Mycobacteriaceae* with *Bacteriaceae*.

Fischer (1903) recognized the two orders *Haplobacterinae* and *Trichobacterinae*.

Erwin F. Smith (1905) followed Migula's (1900) scheme of ordinal designation, but added a third order, *Myxobacteria*.

The discovery by Schaudinn (1905) of the causal organism of syphilis and the interest during the past decade in the relapsing fevers and the protozoan diseases has called particular attention to the spiral microorganisms, particularly the flexuous forms usually termed spirochetes. There is no agreement at the present time as to the position of these forms either among the true bacteria or the protozoa. Blanchard (1906) put the genus *Spirochaeta* with *Trypanosoma* in the *Trypanosomidae*. Swellengrebel (1907) included these forms with the bacteria in the

Spirillaceae. Doflein (1911) placed them among the protozoa. Dobell (1911) used the group name *Spirochaetoidea*. Gross (1912) included them under *Spirohemaceae*, as did also Gonder (1914).

Lotsy (1907) followed the bacterial grouping proposed by Fischer, but added *Myxobacteria* as a coördinate order.

The work of Ellis (1907) and of Molisch (1910) has emphasized the sheathed filamentous or iron bacteria and their importance as a bacterial group.

Jensen (1909) has proposed that the bacteria be divided into the two orders *Cephalotrichinae* and *Peritrichinae*, the former to include those bacteria which are the more primitive and are typically water forms; endospores produced only in a few sulphur free bacteria; cells spherical, rod shaped or spiral; securing their growth energy almost exclusively by oxidative processes; cells motile or non motile, if the former the flagella polar, never diffuse. In the *Peritrichinae* on the other hand, the cells are either spherical or rod shaped, never spiral; peritrichous or non-motile; not typically primitive water forms and usually not securing growth energy solely by oxidative processes.

Heim (1911) differentiates between the true bacteria or *Schizomycetes* and the thread bacteria or *Trichomycetes*.

Kolle and Hetch (1911) recognize the *fission fungi*, divided into Cocci, Bacilli and Spirilla, and the *fission algae* including the sulfur bacteria, the iron bacteria and the *Streptothricaceae*.

Schneider (1912) divides the *Schizomycetes* into seven coördinate families, *Coccaceae*, *Bacteriaceae*, *Spirillaceae*, *Spirochaetaceae*, *Mycobacteriaceae*, *Chlamydobacteriaceae* and *Beggiatoaceae*.

Benecke (1912) recognizes two orders, *Haplobacterinae* with six families and *Desmobacterinae* with one family.

Engler (1912) differentiates the *Eubacteria* with six families and *Thiobacteria* with two families.

Vuillemin (1913) insists that the group *Microsiphonees* including the higher filamentous forms should be separated from the *Schizomycetes*.

A review of these groups show them to be based in the various classifications upon different characteristics. Unfortunately but

few authors have included all the forms commonly grouped with the bacteria, so that the classifications do not coincide in the types considered.

Some authors (as Cohn (1872), Zopf (1883), Flügge (1886), De Toni and Trevisan (1889), Ludwig (1892), Hueppe (1895), Migula (1897), Chester (1901), Kendall (1902), Schneider (1912)) based their primary groups upon the shape of the bacterial cells, usually recognizing filamentous forms as one of the groups. This in the various classifications gave rise to from three to six or eight coördinate groups.

A few authors (De Bary (1884), Hueppe) have differentiated organisms as endosporous and arthrosporous. A fuller knowledge of the life history of the various microörganisms has led to an abandonment of this grouping as not tenable.

The work of Winogradsky (1888) and others on the sulphur bacteria has led some authors (as Migula (1900), E. F. Smith (1905) Engler (1912)) to recognize the true bacteria (*Eubacteria*) and the sulphur bacteria (*Thiobacteria*), as primary coördinate groups.

The studies of Thaxter (1892 *et al*) has induced a few authors to recognize the Myxobacteria as an important group. Among such are Lotsy (1912), Smith (1905) and Engler (1912).

The differentiation of bacteria on the basis of true filament production (not merely chain formation) was first suggested by Cohn (1875) and has been used as a primary grouping by De Toni and Trevisan (1889), Fischer (1895), Lehmann and Neumann (1896), Fischer (1903), Lotsy (1907), Heim (1911), Benecke (1912) and Vuillemin (1913). In many respects this has appealed more strongly than any other basis of differentiation to a majority of taxonomists in recent years.

The suggestion of Jennings that bacteria should be separated into those which divide longitudinally and those which divide transversely has never met with favor. The order *Paraschizae* was based upon Metchnikoff's (1888) genus *Pasteuria* which is generally regarded as not belonging with the bacteria and the genus *Astrobacter* described by Jennings based upon stained mounts from stagnant water prepared to show the flagella of

Spirillum undula. This latter genus *Astrobacter* was never recognized in a living condition. The evidence that bacteria were actually observed is by no means conclusive. Jennings' grouping can therefore scarcely be regarded as valid. However, it is possible that the differentiation might be revived for the separation of the true bacteria and the forms more closely related to the protozoa.

The evidence brought forward by Schaudinn (1905) and his followers in the study of the spirochetes makes it probable that they should either be located definitely among the protozoa or as a main group among the bacteria showing many intermediate characters.

The work of Ellis (1907) and of Molisch (1910) has emphasized the individuality of the iron bacteria, justifying certain of the earlier writers in regarding them as one of the principal groups of the Schizomycetes.

Jensen's classification of bacteria into *Cephalotrichinae* and *Peritrichinae* has much that is attractive, but a careful study of his proposed groupings shows that they are not well defined.

It would seem from a review of the literature and a consideration of the characteristics of the organisms that the following principal groups may be recognized among the bacteria or *Schizomycetes*:

1. The true bacteria which include the forms most commonly studied in the laboratory; they are probably more primitive than other more highly differentiated groups.

2. The thiobacteria characterized by certain relationships to sulphur. They all grow best in the presence of hydrogen sulphid, and always contain sulphur granules or bacteriopurpurin or both.

3. The myxobacteria showing a pseudoplasmodial stage, and fruiting stages resembling in some respects those of the slime molds.

4. The iron bacteria, usually sheathed, frequently growing in water containing iron and with a deposit of iron oxid in the sheath; typically water forms without true branching, showing relationships with the algae.

5. The thread bacteria or ray fungi which show a filamentous form, frequently with true branching. Not water forms. As a group intergrading with the fungi.

6. The spirochetes, slender organisms usually spiral and frequently flexuous, showing many characteristics relating them to the protozoa.

In each of the groups here indicated, except the true bacteria, there is a definite specialization in some direction; forms which are close to the true bacteria are to be found in each group, while others within the group may show an approach to the algae, the fungi or the protozoa.

If the group *Schizomycetes* is to be regarded as a class, the subgroups should receive ordinal names. They may be termed the *Eubacteriales*, *Thiobacteriales*, *Myxobacteriales*, *Chlamydobacteriales*, *Actinomycetales* and *Spirochaetales*, respectively.

The following key to these orders gives the most striking of the differential characters.

- A. Plant-like in the principal characters, not protozoan like, cells never slender, flexuous spirals; cell division never longitudinal.
 - I. Not producing a pseudoplasmodium during the vegetative stage; without a highly developed, cyst-producing, resting stage.
 - a. Containing neither granules of free sulphur, nor bacteriopurpurin, nor requiring the presence of hydrogen sulphid for the best development.
 - 1. Not typically producing filaments as a regular growth form, though chains of cells may be developed. Conidia not developed, spores when formed are endospores.

Order I. *Eubacteriales*
 - 2. Typically producing true filaments as a regular growth form. Conidia may be developed, but never endospores.
 - (a) Alga-like, typically water forms. Filaments never showing true branching; false branching may be present. A sheath usually evident, and usually impregnated with iron.

Order II. *Chlamydobacteriales*
 - (b) Mold like, not typically water forms, nor with the sheath impregnated with iron. True branching often evident.

Order III. *Actinomycetales*
 - b. Cells typically containing either granules of free sulphur or with bacterio-purpurin or both, usually growing best in the presence of hydrogen sulphid.

Order IV. *Thiobacteriales*

- II. Cells united during the vegetative stage into a pseudoplasmodium which passes over into a highly developed, cyst-producing, resting stage.

Order V. *Myxobacterales*

- B. Protozoan-like in many characters. Cells usually relatively slender flexuous spirals; multiplication of cells apparently by longitudinal division in some types, by transverse division in others, or both.

Order VI. *Spirochaetales*

REFERENCES

- BENECKE, WILHELM 1912 Bau und Leben der Bakterien.
 BLANCHARD, R. 1906 Spirilles, spirochetes et autres microorganismes à corps spirale. La Semaine Medicale, **26**, 1.
 CHESTER, F. D. 1897 Classification of the Schizomycetes. Annual Report Delaware College Agricultural Experiment Station, **9**, 62.
 COHN, FERDINAND 1872 a Organismen in der Pockenlymphe. Virchow's Archiv, **55**, 229-238.
 COHN, FERDINAND 1872 b Untersuchungen über Bakterien. Beiträge zur Biologie der Pflanzen, **1** (Heft 1), 127-224.
 COHN, FERDINAND 1875 Untersuchungen über Bakterien, II. Beiträge zur Biologie d. Pflanzen, **1** (Heft 3), 141-208.
 DEBARY, A. 1884 Vergleichende Morphologie und Biologie der Pilze, Mycetozoa und Bakterien. Leipzig.
 DETONI, J. B., AND TREVISAN, V. 1889 Schizomycetaceae, in Saccardo's Sylloge Fungorum, **8**, 923-1087.
 DOBELL, C. CLIFFORD 1911 On *Cristispira veneris* nov. sp. and the affinities and classification of the spirochaetes. Quarterly Journal of Microscopical Science **56**, 507-540.
 DOFLEIN, F. 1911 Lehrbuch der Protozoenkunde. Jena.
 ELLIS, DAVID 1907 A contribution to our knowledge of the thread bacteria. Cent. f. Bakt., Par. u. Inf., Abt. 2, **19**, 516.
 FISCHER, ALFRED 1895 Untersuchungen über Bakterien. Jahresb. f. wiss. Botanik, **27**, 1-163.
 FISCHER, ALFRED 1903 Vorlesungen über Bakterien. Ed. 2.
 FLÜGGE, C. 1886 Die Mikroorganismen. Leipzig.
 GONDER, RICHARD 1914 Spironemacea (Spirocheten), in Prowazek's Handbuch der pathogenen Protozoen. Lief. **6**, p. 671.
 GROSS, J. 1912 Ueber Systematik, Struktur und Fortpflanzung der Spironemacea. Cent. f. Bakt., Par., u. Inf., Abt. 1., **65**, 83.
 HEIM, LUDWIG 1911 Lehrbuch der Bakteriologie. Ed. 4.
 HUEPPE, F. 1886 Die Formen der Bakterien und ihre Beziehungen zu den Gattungen und Arten. Wiesbaden.
 HUEPPE, F. 1891 Die Methoden der Bakterien-Forschung. Ed. 5. Wiesbaden.
 HUEPPE, F. 1895 Principles of bacteriology, translated by E. O. Jordan.
 JENNINGS, A. VAUGHN 1899 On a new genus of bacteria (*Astrobacter*). Proc. Royal Irish Academy, Ser. 3, **5**, 315.
 JENSEN, ORLA 1909 a Die Hauptlinien des natürlichen Bakteriensystems. Cent. f. Bakt., Par. u. Inf., Abt. 2, **22**, 305-346.

- JENSEN, ORLA 1909 b Vorschlag zu einer neuen bakteriologischen Nomenklatur. Cent. f. Bakt., Par. u. Inf., Abt. 2, **24**, 477.
- KENDALL, ARTHUR I. 1902 A proposed classification and method of graphical tabulation of the characters of bacteria. Public Health, **28**, 414.
- KOLLE and HETSCH 1911 Bakteriologie.
- LEHMANN, K. B. AND NEUMANN, R. O. 1896 Atlas und Grundriss der Bakteriologie. München.
- J. P. LOTSY 1907 Vorträge über botanische Stammesgeschichte Vol. I. Algen und Pilzen.
- LUDWIG, FRIEDRICH 1892 Lehrbuch der niederen Kryptogamen.
- METCHNIKOFF, ELIE 1888 *Pasteuria ramosa*, un représentant des bacteries à divisione longitudinale. Ann. de l'Inst. Pasteur, **2**, 166.
- MIGULA, W. 1894 Ueber ein neues System der Bakterien. Arb. a. d. Bakt. Inst. d. tech. Hochschule zu Karlsruhe, **1**, 235-238.
- MIGULA, W. 1895 Schizomycetes. In Engler and Prantl's Natürlichen Pflanzenfamilien.
- MIGULA, W. 1900 System der Bakterien. Vol. 1, 1897. Vol. 2, 1900.
- MIGULA, W. 1904 Allgemeine Morphologie, Entwicklungsgeschichte, Anatomie und Systematik der Schizomyceten. In Lafar's Handbuch der tech. Mykologie. Ed. 2.
- MOLISCH, HANS 1910 Die Eisenbakterien. Jena.
- NAEGELI, CARL WILHELM VON 1857 Bericht über die Verhandlungen der bot. Section d. 33 Versammlung deutscher Naturforscher. Botanische Zeitung **15**, 760.
- SCHNEIDER, A. 1912 Pharmaceutical Bacteriology.
- SCHRÖTER, J. 1886 Die Pilze, in Cohn's Kryptogamen Flora von 'Schlesien.
- SMITH, ERWIN F. 1905 Bacteria in relation to plant diseases. Vol. 1.
- SWELLENGREBEL, M. 1907 Sur la Cytologie comparée des Spirochetes. Ann. de l'Inst. Pasteur, **21**, 448 and 562.
- THAXTER, ROLAND 1892 On the Myxobacteriaceae, a new order of Schizomycetes Bot. Gaz., **17**, 394.
- VUILLEMIN, PAUL 1913 Genera Schizomycetum. Annales Mycologici, **11**, 526.
- WINOGRADSKY, SERGIUS 1888 Beiträge zu Morphologie und Physiologie der Bakterien, Heft I, Zur Morphologie und Physiologie der Schwefelbakterien. Leipzig.
- WINTER, GEORG 1880 Die Pilze in Rabenhorst's Kryptogamenflora. Ed. 2, Vol. I.
- ZOPF, W. 1883 Die Spaltpilze. Ed. 1.
- ZOPF, W. 1885 Die Spaltpilze. Ed. 3.